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Vittaria appalachiana: A Name for the "Appalachian Gametophyte"

DONALD R. FARRAR
Department of Botany, Iowa State University, Ames, IA 50011

JOHN T. MICKEL
New York Botanical Garden, Bronx, NY 10458

Several fern species are known to exist over parts of their range as gametophytes only, without development of the sporophyte stage of their life cycle. Gametophytes of *Hymenophyllum wrightii* Bosch have been collected at several points along the Pacific Coast from Southeast Alaska to Vancouver Island whereas sporophytes of this species in North America are known only from the Queen Charlotte Islands (Iwatsuki, 1961; Taylor, 1967). Also in the Hymenophyllaceae, Farrar, Parks, & McAlpin (1982) have demonstrated the occurrence of populations of *Trichomanes* gametophytes in New England over 800 km from any known sporophyte of the genus, and Pittillo et al. (1975) noted the presence of gametophytes of *Hymenophyllum* in the gorges of the Southern Appalachian Mountains up to 40 km from the single locality for *H. tunbrigense* (L.) Smith in Pickens Co., South Carolina. In each of these cases, the gametophytes have the characteristic of producing gemmae by which they maintain local populations vegetatively and independently of the sporophyte generation.

Species of *Vittaria*, the shoestring ferns, also have gemma-producing gametophytes. In the continental United States, *Vittaria* is represented by three species. In peninsular Florida, *V. lineata* (L.) Smith is common on trunks of cabbage palms in both gametophyte and sporophyte stages. Here gametophytes produce the gemmae characteristic of the genus, but also produce sporophytes in a normal sexual life cycle (Farrar, 1974, 1978). Gametophytes of the common Central American species, *V. graminifolia* Kaulf., have been collected from bases of beech trees in southern Alabama (Farrar & Landry, 1987).

In the Appalachian Mountains and Appalachian Plateau regions of the eastern United States, a third species of *Vittaria* is represented by the gametophyte stage only. It is distinct from the gametophytes of the other two species. It is a common and conspicuous, though often unrecognized, component of the vegetation of cool, moist, heavily shaded outcroppings of non-calcareous rock. A detailed description of these plants and their habitat has been presented by Farrar (1978) along with a discussion of unsuccessful attempts by Farrar and others to induce these plants to produce normal sporophytes in culture. It is this species, commonly known as the "Appalachian Gametophyte" or "Appalachian *Vittaria* Gametophyte," for which we propose the new Latin binomial, *Vittaria appalachiana*.

Vittaria appalachiana was first recognized as the gametophyte of a fern by A. J. Sharp in 1930. Wherry suspected it to be an unknown species of

Hymenophyllum (Wherry, 1942), and Wagner & Sharp (1963) assigned it to the genus *Vittaria*.

However, Sharp was not the first to discover the Appalachian gametophyte. An herbarium specimen at the New York Botanical Garden, collected in 1824 by Schweinitz in North Carolina, bears the name *Jugermannia laciniata*. Apparently the name was never published; it does not appear in any of Schweinitz' publications nor on any specimens in his herbarium (at PHIL) nor among his catalogs or notes at the Philadelphia Academy of Natural Sciences.

Wagner & Sharp (1963) suggested that the Appalachian plants were possibly gametophytes of *V. lineata*. However, Farrar (1978) found significant morphological differences between the Appalachian plants and gametophytes of *V. lineata*, especially in the pattern of gemma production. These differences, as well as the inability of Appalachian plants to produce sporophytes, are maintained when Appalachian and Florida gametophytes are grown in common culture.

The Appalachian plants produce gemmae in pairs, a basal gemma supporting at its tip a second gemma (Fig. 1d). Of American species in which the gametophytes have been studied, this pattern is characteristic of species of the subgenus *Euvittaria* as recognized by Benedict (1914) (= subg. *Vittaria*) (Fig. 2a,b). In the three species so far examined of Benedict's other subgenus, *Radiovittaria*, gemmae do not subtend additional gemmae (Fig. 2c). Thus the Appalachian *Vittaria* likely belongs to subgenus *Vittaria*. In starch gel enzyme electrophoresis comparisons, Farrar (1985) found that the Appalachian *Vittaria* shared fewer than 50% of its alleles with any one of *V. lineata*, *V. graminifolia*, or *V. dimorpha*, the three common Central American species of subgenus *Vittaria*.

Enzyme genotypes of the Appalachian plants also revealed typical variation between populations of different habitats but a very high degree of genetic uniformity within habitats, indicating very little gene flow, even between nearby habitats (Farrar, 1990). Farrar, Parks & McAlpin (1983) pointed out that the occurrence of Appalachian gametophytes is limited to habitats near and south of the limits of Pleistocene glaciation. The low dispersal ability demonstrated both by this distribution and by the high fixation of genotypes within habitats suggests long residence of the Appalachian plants in the eastern United States and probable genetic divergence of the Appalachian plants from their tropical relatives. Sporophytes of *V. appalachiana* could, in fact, be extinct.

Gastony (1977) reported the chromosome number of *Vittaria* gametophytes from Indiana as 120, equalling the common 2n number of the genus. Stokey (as reported by Farrar, 1978) obtained several abortive embryos and young sporophytes through her attempts to culture the Appalachian plants and concluded these were produced apogamously. Farrar (1978) observed similar abortive young sporophytes in collections from Ohio. Although rendering chromosome numbers inconclusive as determinants of specific relations, taken together with observations of fixed heterozygosity at some gene loci, these observations led Farrar (1990) to include interspecific hybridization with

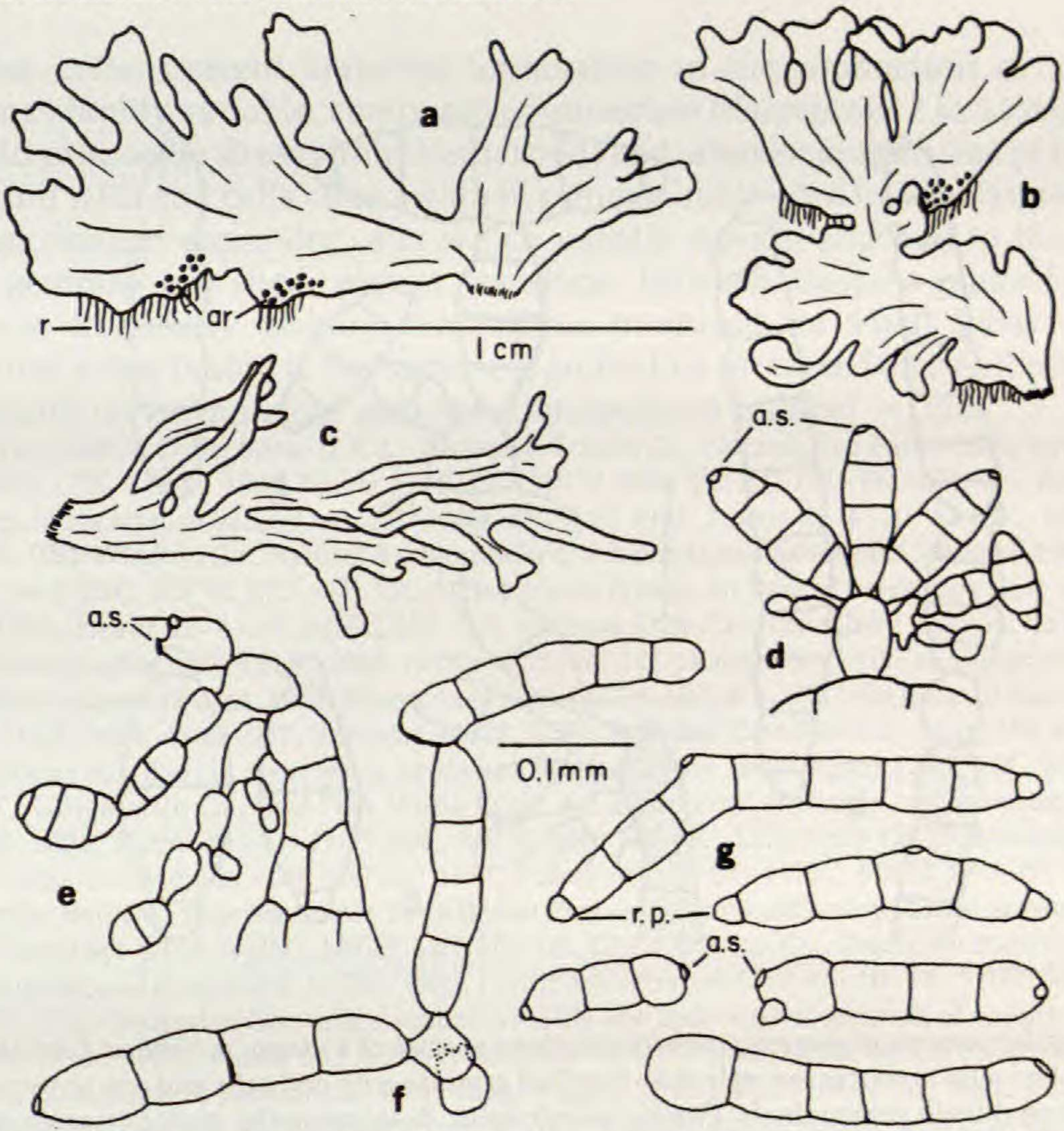

FIG. 1. *Vittaria appalachiana* gametophytes. **a.** Large plant bearing rhizoids and archegonia at its base and aerial gemma-producing branches. **b.** Plant in which an aerial branch has proliferated into a second large plant bearing archegonia and rhizoids. **c.** Etiolated growth form typical of darkest habitats. **d.** Relatively regular pattern of gemma production in which basal gemmifer supports additional gemmifers and up to 8 pairs of gemmae. **e.** Gemmiferous apex in which thallus gemmifers, and gemmae are not clearly differentiated. **f.** Cluster of gemmae and gemmifers abnormally abscised. **g.** Mature gemmae showing typical variation in form and size. ar = archegonia a.c. = abscision scar r = rhizoid r.p. = rhizoid primordium

production of diploid gametophytes as a possible origin of the Appalachian *Vittaria* gametophytes.

It may yet be shown that the Appalachian *Vittaria* gametophytes are most closely related to and possibly derived from a particular extant New World species of *Vittaria*. However, our current assessment is that they are genetically distinct from all other named species. This genetic distinction is expressed through morphological and physiological characteristics and habitat preference, and possibly results from an ancient origin and long isolation in upland eastern North America. The Appalachian *Vittaria* gametophytes are common and well known plants of this region and need a specific name.

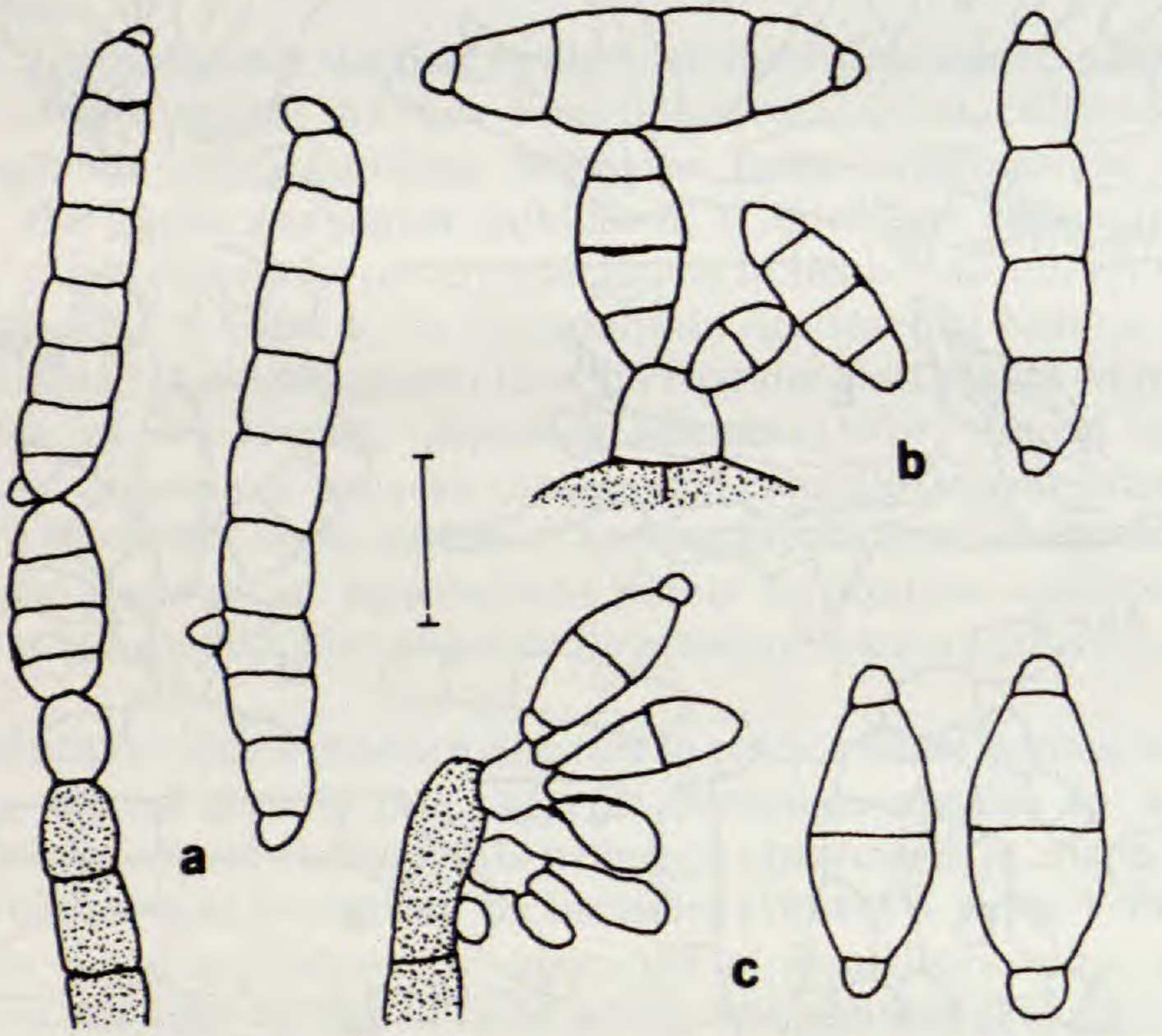

FIG. 2. Regular patterns of gemma production in three species of *Vittaria*. **a.** *Vittaria lineata*. Basal gemmifer typically produces one pair of 6–16 celled gemmae with end cells and one or two medial cells bearing rhizoid primordia. **b.** *Vittaria graminifolia*. Basal gemmifer typically produces two pairs of 6 celled gemmae with the end cells differentiated as rhizoid primordia. **c.** *Vittaria stipitata*. Basal gemmifers produce up to three 4 celled gemmae with end cells differentiated as rhizoid primordia. Production of gemmae not in interconnected pairs is typical of subgenus *Radiovittaria*.

Vittaria appalachiana Farrar & Mickel, sp. nov.—TYPE: Ohio, Hocking Co., Cedar Falls, in crevices and grottos of sandstone cliffs, 7 Aug. 1987, *Farrar 87–8–7–2* (holotype ISC; isotypes MICH, MO, NY, UC, US). (Fig. 1).

Tantum in statu gametophytico existens. Thallus unam cellulam crassus, erectus, ramosus, ecostatus. Rhizoidea secus marginem et paginam inferiorem juxta substratum. Meristemata ramorum rotundata, gemmipara. Gemmae filamentosae, 2–12 cellulas longae. A *Vittaria lineata* ceterisque generis speciebus gemmis irregularibus et cellulis gemmarum et gemmiferis in illas thalli pluries transientibus differt.

Sporophyte lacking. Gametophyte green, epipetric or occasionally epiphytic, perennial and clone-forming by vegetative reproduction. Meristem of individual plants discontinuous, marginal on rounded branch apices; mature form consisting of a branched, ribbon-like thallus one cell in thickness, usually differentiated into basal and upright branches; basal branches attached to the substrate by numerous short, brown rhizoids emanating from marginal and interior cells; upright branches terminating in the production of gemmae. Gemmae highly variable, composed of uniseriate filaments of 2 to 12 cells, with rhizoid primordia absent from medial cells and often lacking on one or both end cells and with end cells often swollen; gemmae subtended by specialized round or flask-shaped gemmifer cells which usually remain attached to the thallus after gemmae are shed; abrupt transition between thallus, gemmifers, and gemmae frequently lacking. Archegonia produced on small lobes of basal branches, often buried in the substrate; antheridia produced on small plants and especially on germinating gemmae. Chromosome number = 120.

Representative Collections: U.S.A.: **Alabama**: Ettowa Co., Noccollulah Falls, under overhanging sandstone cliff, 7 Sept. 1968, *Farrar 1186* (ISC, MICH, MO, NY, UC, US): Franklin Co., Rock Bridge Canyon, in rockhouse behind natural bridge, 29 April 1982, *Farrar 82–4–29–13* (ISC, MICH, MO, NY, UC, US); Winston Co., Natural Bridge, under overhanging sandstone cliff, 28 April 1982, *Farrar 82–4–28–3* (ISC, MICH, MO, NY, UC, US); Natural Bridge, on base of beech tree near stream, 28 April 1982, *Farrar 82–4–28–6* (ISC, NY, US); **Georgia:** Dade Co., Cloudland Canyon, on coal seam under overhanging cliff, 6 Sept. 1968, *Farrar 1185* (ISC, NY); Rabun Co., Tullulah Gorge, on quartzite and schist ledges, 22 Sept. 1968, *Farrar 1246* (ISC, MICH, MO, NY, UC, US); gorge of Big Creek, just below High Falls, Aug. 1957, *Schuster 40037*, (ISC); **Indiana:** Crawford Co., along US 460, 1 mile east of Perry Co. line, in crevices in sandstone bluffs, 12 July 1969, *Farrar 1263*, (ISC, MICH, MO, NY, UC, US); Martin Co., East Fork White River, 4.2 miles north of Shoals, under sandstone cliffs, 11 Nov. 1981, *Farrar 81–11–11–1* (ISC, MICH, MO, NY, UC, US); Perry Co., Penitentiary Rocks, under large overhanging cliff, 13 Nov. 1981, *Farrar 81–11–13–4* (ISC, MICH, MO, NY, UC, US); **Kentucky:** Bell Co., Pine Mountain State Resort Park, sandstone cliffs along small stream, 16 Aug. 1989, *Farrar 89–8–16–3* (ISC, MICH, MO, NY, UC, US); Christian Co., Pennyrile State Park, under overhanging sandstone cliffs, 16 Oct. 1985, *Farrar and Johnson-Groh 85–10–16–1* (ISC, MICH, MO, NY, UC, US); Crittenden Co., under sandstone cliffs one mile west of junction of county roads 120 and 139, 17 Oct. 1985, *Farrar and Johnson-Groh 85–10–17–1* (ISC, MICH, MO, NY, UC, US); Hardin Co., one mile north of Summit, 27 Nov. 1954, *Wagner 8012* (ISC); Powell Co., Nada Tunnel, back of rockhouse above east entrance to tunnel, 30 Aug. 1989, *Farrar 89–8–30–9* (ISC, MICH, MO, NY, UC, US); Wolfe Co., Rock Bridge Recreation Area, under small cliff at natural bridge, 31 Aug. 1989, *Farrar 89–8–31–2* (ISC, MICH, MO, NY, UC, US); Tiglet Holler, between overhanging ledges of sandstone, 5 Oct. 1946, *Fulford s.n.* (ISC); **New York:** Cattaraugus Co., Rock City Park, in large rockhouses of Pottsville sandstone, 3 Aug. 1983, *Parks 4295* (MVSC); Chautauqua Co., Panama Rocks, undersides of sandstone boulders, 6 Aug. 1986, *Farrar and Johnson-Groh 86–8–6–3* (ISC, MICH, MO, NY, UC, US); **North Carolina:** Avery Co., Linville Falls, under overhanging cliffs below upper falls, 25 Aug. 1989, *Farrar 89–8–25–2* (ISC, MICH, MO, NY, UC, US); Burke Co., South Mountain State Park, cliffs along cascades on Shinny Creek, 19 Aug. 1989, *Farrar 89–8–19–3* (ISC, MICH, MO, NY, UC, US); Graham Co., Joyce Kilmer Memorial Forest, vertical surface of grauwhacke boulder along Grassy Ridge Trail, July 1971, *Pittillo and Hyatt 4234* (ISC); Macon Co., Dry Falls, under cliffs along trail to falls, 21 Aug. 1989, *Farrar 89–8–21–6* (ISC, MICH, MO, NY, UC, US); Glenn Falls, 14 July 1984, *Johnson-Groh s.n.* (ISC, MICH, MO, NY, UC, US); Highlands Falls, shaded cliffs by falls, 17 Aug. 1951, *Anderson 10407* (ISC); Horse Cove, 4 miles southeast of Highlands, on bark at base of tree, 18 Aug. 1951, *Anderson 10422* (ISC); Stokes Co., Hanging Rock State Park, on cliffs at cascades, 26 Aug. 1989, *Farrar 89–8–26–9* (ISC, MICH, MO, NY, UC, US); Swain Co., Clingman's Dome Road, 10 miles west of dome, under small rock overhangs, elev. 4000 ft., 23 Sept. 1968, *Farrar 1254* (ISC, MICH, NY, US); Yancey Co., Clingman's Peak near Mt. Mitchell, moist crevices of non-calcareous rock, 5 Oct. 1957, *Sharp F571* (ISC); **Ohio:** Lake Co., Little Mt, Holden Arboretum, dark moist faces of Sharon Conglomerate, 10 June 1982, *Cusick 21673* (ISC); Little Rocky Hollow, under overhanging sandstone cliffs, 9 Aug. 1987, *Farrar 87–8–9–6* (ISC, MICH, MO, NY, UC, US); Shiek Hollow, under overhanging sandstone cliffs, 9 Aug. 1987, *Farrar 87–8–9–2* (ISC, MICH, MO, NY, UC, US); Jackson Co., St. Catherine's Preserve, sandstone cliffs along Salt Creek Trail, 8 Aug. 1987, *Farrar 87–8–8–2* (ISC, MICH, MO, NY, UC, US); **Pennsylvania:** Lancaster Co., Kelly's Run, under outcrops of schist along creek, 22 Sept. 1981, *Farrar 81–9–22–7* (ISC, MICH, MO, NY, UC, US); Lawrence Co., McConnel's Mill State Park, under sandstone ledges along Slipper Rock Creek, 21 Oct. 1981. *Farrar 81–10–21–6* (ISC, MICH, NY, US); York Co., Otter Creek Recreation Area, under outcrops of schist along creek, 22 Sept. 1981, *Farrar 81–9–22–13* (ISC, NY, US); **Tennessee:** Blount Co., The Sinks along route 73, under rock ledges, 15 May 1966, *Farrar 1051* (ISC, NY); Cumberland Co., Obed River northeast of Crossville, wet crevices of sandstone bluffs, 15 Aug. 1951, *Norris and Sharp 16193* (ISC); Johnson Co., six miles west of Damascus, VA, 28 Aug. 1984, *Renzaglia s.n.* (ISC); Sevier Co., Alum Cave, moist surface of cliffs above parking lot, 8 March 1952, *Sharp 16393* (ISC); Ramsey Cascades, wet undersides of overhanging cliff, 16 July 1974, *Sharp 5626* (ISC); **Virginia:** Dickenson Co., Breaks Interstate Park, sandstone bluffs along Laurel Creek, 6 July 1978, *Farrar 78–7–6–1* (ISC, MICH, MO, NY, UC, US); Giles Co., Bear Cliffs on Salt Pond Mountain, crevices in cliffs of small box canyon, 28 Aug. 1989, *Farrar 89–8–28–1* (ISC, NY, US); Washington Co., Highway 58, 5 miles west of Konnarock, 25 Aug. 1989, *Farrar 89–8–25–4* (ISC, MICH, MO, NY, UC, US); **West Virginia:** Pocohontas Co., upper falls of Hills Creek, 5 miles west of visitor's center, Monangahela National Forest, under deep rock overhangs, 12 Aug. 1970, *Wagner 70394* (ISC); Tucker Co., Blackwater Falls, in crevices near falls, 15 Sept. 1972, *Mc Alpin 2037* (ISC).

This species is distinguished from other *Vittaria* species by the absence of sporophytes and by an irregular pattern of gemma production (Fig. 1). Gemma form and size varies widely as does the number of gemmae and additional gemmifers produced by a basal gemmifer and the site of dehiscence. Structures intermediate between gemmae, gemmifers and thallus cells are common. In contrast, gemmae of *V. graminifolia* are regularly composed of 6 cells with each end cell differentiated into small rhizoid primordia and with basal gemmifers regularly producing two pairs of gemmae (Fig. 2b) (Farrar, 1974; Sheffield & Farrar, 1988). Gemmae of *V. lineata* are composed of 4 to 16 cells with rhizoid primordia often differentiated on 1 or 2 medial cells as well as the end cells, and with basal gemmifers producing one or two pairs of gemmae (Fig. 2a) (Farrar, 1974). Both of these species display clear differentiation between thallus, gemmifer, and gemma cell types.

Vittaria appalachiana can be found on cool, moist, heavily shaded outcroppings of non-calcareous rock and occasionally on nearby tree bases, from southern Indiana, northeastward across southern and northeastern Ohio to southwestern New York and southeastern Pennsylvania, south along the Appalachian Mountains and Appalachian Plateau to northern Georgia and Alabama and westward to central Tennessee and west-central Kentucky.

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Review

Developmental Biology of Fern Gametophytes by Valayamghat Raghavan. Developmental and Cell Biology Series, Cambridge University Press, New York. 1989. 361 pp. ISBN 0–521–33–22.

The purpose of this series is to provide relatively short, critical accounts of areas of developmental and cell biology. They are aimed at an audience of advanced undergraduates and graduate students and for biologists who attempt to keep current in related fields that might impact their particular research emphasis. This work meets that purpose for its defined audience, and then some. The distillation of information contained in the references cited on 49 pages of bibliography supports the notion that fern gametophytes provide convenient organisms to study significant problems in biology. The spore and gametophyte plant provide many opportunities to develop model systems to explore basis phenomena in germination, planar growth, initiation of sexual growth from vegetative growth, and gametogenesis, as well as pheromones, breeding and mating systems, apogamy, and apospory. In the first nine chapters, the emphasis is on the morphological, cytological, physiological, biochemical, and molecular changes that occur during the gametophyte generation. In the last five chapters phenomena with evolutionary implications of interest to geneticists, ecologists, and population biologists are treated. This book is complementary to an earlier book in this series by Raghavan on Embryogenesis in Angiosperms: A Developmental and Experimental Study. Individually and together, they constitute a significant compilation of research on the haploid generation and early development of the sporophyte.–JAMES H. PECK, Department of Biology, University of Arkansas at Little Rock, Little Rock, AR 72204.